The Report Committee for Rachel Anne Voyt
Certifies that this is the approved version of the following Report:

Factors affecting the expression of female-biased power in Verreaux's sifaka (*Propithecus verreauxi*)

and

Monomorphism in mammals: A review of current hypotheses

APPROVED BY
SUPERVISING COMMITTEE:

Rebecca Lewis, Supervisor

Anthony Di Fiore

Factors affecting the expression of female-biased power in Verreaux's sifaka (*Propithecus verreauxi*)

and

Monomorphism in mammals: A review of current hypotheses

by

Rachel Anne Voyt

Report

Presented to the Faculty of the Graduate School of

The University of Texas at Austin

in Partial Fulfillment

of the Requirements

for the Degree of

Master of Arts

The University of Texas at Austin

May 2018

Dedication

To Fi, and all that you represent.

Acknowledgements

First and foremost, I would like to thank my advisor, Rebecca Lewis, for her guidance and patience throughout the completion of this report. I would also like to thank Anthony Di Fiore and Chris Kirk for their advice and helpful comments on the project. Finally, to my fellow graduate students, friends, and family – I could not have asked for a better support system. Data for the first chapter of this report was collected with the permission of the Madagascar government and Madagascar National Parks, and the University of Antananarivo and MICET (Madagascar Institute pour la Conservation de Ecosystemes) facilitated the data collection process. Many thanks to the Ankoatsifaka Research Station field team, whose efforts collected much of the data presented here.

Abstract

Factors affecting the expression of female-biased power in Verreaux's sifaka (*Propithecus verreauxi*)

and

Monomorphism in mammals: A review of current hypotheses

Rachel Anne Voyt, M.A.

The University of Texas at Austin, 2018

Supervisor: Rebecca Lewis

The master's report presented here is a compilation of two distinct papers. Their respective abstracts are presented below.

Chapter 1. The development and maintenance of power structures are influenced by multiple interacting variables associated with fighting ability or leverage. However, the relative influence of these variables on the expression of female power within the female-biased power structures that characterize most lemur species is still not well understood. This study examines the potential influence of factors associated with female reproductive costs and leverage on the expression of female power over males in Verreaux's sifaka (*Propithecus verreauxi*) in a combined test of the energy conservation, cost asymmetry, and leverage hypotheses. The leverage hypothesis, but not the energy conservation or cost asymmetry hypotheses, were fully supported. These results suggest that female-biased power structures in lemurs may depend upon female leverage, but not

body mass differences or energy needs. Future studies incorporating physiological measures of female energetics and reproductive stages as well as additional sources of fighting ability other than body mass are necessary to validate this claim.

Chapter 2. Monomorphism in mammals is relatively understudied despite characterizing numerous mammalian species. In this review, I reevaluate the extent of size monomorphism among mammals and examine the existing hypotheses put forward to explain this morphological pattern. I show that monomorphism is likely more common than is typically represented in the literature, while dimorphism is overestimated. Hypotheses explaining monomorphism specifically are rare, however, and must be extrapolated from hypotheses put forth to explain male-biased dimorphism. Monomorphism is thus expected when sexual selection on male body size is weak or is acting on traits related to speed or agility. Environmental constraints, habitat type, or predation pressure may contribute to the effects of sexual selection and/or place limitations on body size that are unrelated to sexual selection. Species-level comparative work focusing on monomorphic species specifically is necessary to resolve these broad-scale trends associated with monomorphism.

Table of Contents

List of Tables

List of Figures

Chapter 1: Factors affecting the expression of female-biased power in Verreaux's sifaka (*Propithecus verreauxi*)

INTRODUCTION

Dominance is a multidimensional construction imbued with overwhelming importance in behavioral research. While considerable debate exists regarding the definition of dominance (e.g., Rowell, 1974; Bernstein, 1981; Hand, 1986; Lewis, 2002, Langbein and Puppe, 2004; Holekamp and Strauss, 2016), it generally refers to the predictable asymmetry in the outcome of decided agonistic interactions, which by definition must involve submissive behavior that occurs either unprovoked or in response to aggression (Rowell, 1974; Bernstein, 1981). The influence of dominance is thought to extend to myriad aspects of group living, including reproductive success, priority of access to food or mating opportunities, and general maintenance of group dynamics (de Waal, 1986).

While dominance is ultimately a characteristic of relationships (Bernstein, 1981), it is often influenced by physical and/or behavioral traits associated with individuals (i.e., "prior attributes"; Chase et al., 2002), which can then vary by season, context, and other extrinsic factors (Hewitt et al., 2009). The interplay between these parameters and their respective contributions to the formation of dominance relationships can be assessed using the power framework, in which "power" refers to a phenomenon that arises from asymmetries in dyadic relationships derived from differences in both dominance and leverage (Lewis, 2002). Within the power framework, Lewis (2002) regards "dominance" as the combined effect of intrinsic (e.g., body mass, canine size) and derived (e.g., coalitionary support) sources of fighting ability (de Waal, 1989; Chapais, 1992), whereas "leverage" is based upon inalienable resources, such as fertilizable eggs or kinship (Hand,

1986). Dominance and leverage may be further influenced by differences in the relative value a given resource has to particular individuals (Parker and Rubenstein, 1981; de Waal, 1989; Dunham, 2008). Together, these factors can produce lasting dyadic asymmetries by influencing the outcome of conflicts over time and space.

Female-Biased Power Structures

Asymmetries within dyads are often biased toward a particular sex. Female-biased power structures (Lewis, *in press*), usually designated in the literature as "female dominant" social structures, are defined by females consistently exhibiting aggressive but rarely submissive behavior toward males, while males are consistently submissive and rarely aggressive toward females (Pereira et al., 1990). Female-biased power structures are uncommon among mammals (Ralls, 1976; Kappeler, 1993a), but characterize the majority of lemur species (Jolly, 1984; Kappeler, 1993a; Eichmueller et al., 2013; Petty and Drea, 2015).

Several hypotheses have been proposed to explain the prevalence of female power in lemurs, emphasizing the role of a diverse set of potential influences (Jolly, 1984; Richard, 1992; van Schaik and Kappeler, 1996; Wright, 1999; Lewis, 2002; Dunham, 2008). This study aimed to better understand the influence of female reproduction costs (Jolly, 1984; Wright, 1999; Dunham, 2008) and economic power (Lewis, 2002) on the expression of female-biased power structures, focusing three interrelated hypotheses: the "energy conservation hypothesis" (ECH: Jolly, 1984; Wright, 1999), the "cost asymmetry hypothesis" (CAH: Dunham, 2008), and the "leverage hypothesis" (LH: Lewis, 2002). These hypotheses are not mutually exclusive and often overlap considerably in their predictions, though with some important distinctions.

The ECH broadly states that female-biased power structures result from the high energetic demands on reproductive female lemurs due to metabolic and environmental factors (Jolly, 1984; Richard and Nicoll, 1987). Indeed, even females from species typically characterized by male-biased or unbiased power structures have been found to engage in higher rates of aggressive behavior (e.g., Japanese macaques: Schino et al., 2004; bank voles: Ylönen and Horne, 2002) and feeding priority (white-handed gibbons: Barelli et al., 2008) during energetically costly lactation periods. However, energy needs in reproductive female lemurs are assumed to be especially great due to resource constraints imposed by the particularly strong resource seasonality and climate unpredictability of Madagascar (Jolly, 1984; Wright, 1999; Dewar and Richard, 2007). Female-biased power structures are thus thought to exist as an adaptation allowing females to maximize their use of scarce resources (Wright, 1999).

The CAH also proposes that female-biased power structures result from heightened female nutritional demands, but differs from the ECH in its theoretical framework and predictions regarding precisely how female-biased energy needs lead to female-biased power structures. Drawing from game theory, the CAH posits that female-biased power structures in lemurs relies upon intersexual size symmetry (Dunham, 2008), which is common among most lemur species (Kappeler and Fichtel, 2015). Many other species that display female-biased power structures are also characterized by females and males of similar adult average body mass, such as the rock hyrax (Koren et al., 2006) and the rufous elephant shrew (Rathbun, 1979). Using size symmetry as a proxy for equal fighting abilities between females and males, the CAH uses game theory to predict that increased female valuation of resources biases conflict outcomes toward females (Parker and Rubenstein, 1981), which in turn may lead to a female-biased power structure (Dunham, 2008). In the event that valuation of resources is equal and/or body size

differences are present, these differences in body size may then also influence conflict outcome.

The LH is similar to the CAH in its theoretical basis, drawing from the political, economic, and sociological theory embedded within the power framework (Lewis, 2002). The LH also posits that female-biased power structures in lemurs may rely upon equal intersexual fighting abilities via size symmetry (Lewis, 2002). However, rather than asymmetries in resource valuation driving female power, the LH suggests that female-biased leverage ultimately drives the formation of female-biased power structures (Lewis, 2002). While leverage may take many forms (Hand, 1986; Lewis, 2002), the influence of mating opportunities has been particularly well documented with regard to intersexual power dynamics (e.g., Sicotte, 2002; van Noordwijk and van Schaik, 2009; Surbeck and Hohmann, 2013; Hohenbrink et al., 2016) and is the source of leverage examined in this study. Similar to the CAH, in the event that intersexual leverage is approximately equal (i.e., in conflicts outside of the mating season) and/or differences in body size are present, these body size differences are also likely to influence conflict outcome.

While the ECH, CAH, and LH present different ultimate explanations for the existence of female-biased power structures in lemurs, their predictions regarding how female power is mediated on a proximate level highlight the potential influence of similar variables. These predictions and the hypotheses to which they correspond are presented below.

1) Reproductively mature females are more likely to win intersexual conflicts
    a. than reproductively immature females (ECH, CAH, LH),
    b. during years in which females produce offspring (ECH, CAH),
    c. when females hold greater leverage (e.g., during the mating season; LH), and
    d. in feeding contexts (ECH, LH)

2) Females are more likely to win intersexual conflicts when their fighting ability (using body mass as a proxy) exceeds that of their conflict partner (CAH, LH)

I tested the predictions of the ECH, CAH, and LH using an existing long-term behavioral dataset documenting body mass and intersexual agonistic interactions in Verreaux's sifaka (*Propithecus verreauxi*), a lemur species whose social structure is characterized by female-biased power (Richard, 1974; Richard, 1978; Richard and Nicoll, 1987). Females consistently win conflicts against males in both feeding and non-feeding contexts (Jolly, 1966; Richard and Heimbuch; 1975; Richard, 1978; Kubzdela, 1997; Palagi et al., 2008). Both females and males form intrasexual linear dominance hierarchies maintained via unidirectional submissive signals (i.e., chatter vocalizations) (Lewis and van Schaik, 2007) and aggressive interactions (Kraus et al., 1999; Palagi et al., 2008; Norscia and Palagi, 2015). Agonistic interactions generally occur more frequently in the rainy season than the dry season, which may in part be related to the reproductive season or a lack of energy in the dry season due to the depletion of food resources (Richard and Heimbuch, 1975; Richard, 1978).

Reproductive maturity in female Verreaux's sifaka, defined by age at first birth, occurs most commonly at 5 (Kappeler and Fichtel, 2012) or 6 (Richard et al., 2002) years of age. While a small number of females have been observed to give birth as early as age 3, these infants rarely survive, and reproductive success (i.e., infant survival past 12 months) only begins improving after age 6 (Richard et al., 2002). Mating typically takes place during a six-week period within the months of January through March (Brockman et al., 1999; Leimberger and Lewis, 2017), and females are in estrus within a 0.5 to 96 hour window (Brockman et al., 1999). Births occur during the dry season during June to mid-August (Lewis and Kappeler, 2005), and mid/late lactation and weaning take place during the rainy season (Brockman, 1994; Richard et al., 2002; Lewis and Kappeler,

2005). Interbirth intervals are usually 1 to 2 years (Richard et al., 2002). Females incur the greatest energy demands during mid to late lactation periods, which occur early in the rainy season when food availability is greatest (Lewis and Kappeler, 2005; Koch et al., 2017). Verreaux's sifaka exhibit body size monomorphism, with adult females and males exhibiting no significant differences in average body mass (Kappeler, 1990; Ravosa et al., 1993; Richard et al., 2002; but see Lewis and Kappeler, 2005) or limb measurements (Ravosa et al., 1993). Both females and males experience seasonal fluctuations in body mass, although female body mass exhibits a slightly greater decrease during the late dry season (Richard et al., 2000; Lewis and Kappeler, 2005). Understanding how variation in these reproductive and physical states influences intersexual conflicts is needed to improve our understanding of female power in Verreaux's sifaka and the variation in power structures overall.

METHODS

Study Site and Subjects

Data were collected at the Ankoatsifaka Research Station (20º47'17"S, 44º10'0"E) in Kirindy Mitea National Park (KMNP) of western Madagascar. Verreaux's sifaka at KMNP reside in social groups comprising between 2 and 11 (mean = 6) individuals including 1 to 3 adult females and 0 to 3 adult males (Leimberger and Lewis, 2017). A total of 31 females and 33 males living in 4 social groups were observed during the study period, with females ranging from 0 to at least 13 years of age and males ranging from 0 to at least 10 years of age. Because mating bouts were rarely observed and paternity data was not used in this study, male reproductive maturity was assumed to occur at adulthood (age 5) (Richard et al., 2000; Lawler et al., 2003; Lewis and van Schaik, 2007), while females were considered reproductively mature at the age of first observed birth. Because exact birth dates were not always known, but over 90% of births occur during July and August (Lewis and Kappeler, 2005), individuals were assigned to age 1 on September 1 following their birth year and changed age category on September 1 of each following year. When birth years were unknown, minimum individual ages were estimated via body size, tooth wear, and/or nipple condition. A subset of the population is sedated and captured annually in June-July (cf. Lewis, 2009; Rasambainarivo et al., 2014). Morphological measurements, including body mass, and sex assignments based on genital morphology are recorded during these annual captures.

Data Collection

Intersexual agonistic interactions, including initiator, receiver, and duration, were collected using continuous focal animal sampling (Altmann, 1974) in 1-hour samples

from 2007 to 2016. No behavioral data were included from 2009 due to an interruption in data collection caused by Cyclone Fanele (Lewis and Rakotondranaivo, 2011; Lewis and Bannar-Martin, 2012). Conflict outcome was scored for each decided agonistic encounter, defined as conflicts in which i) the winner exhibited only aggressive behaviors and the loser exhibited only submissive behaviors, and ii) the loser exhibited submissive behaviors and the winner exhibited no aggressive or submissive behaviors (Pereira et al., 1990). Because chatter vocalizations are used as a formal submissive signal (Lewis and van Schaik, 2007), only dyadic interactions in which individuals utilized these vocalizations were included in this analysis. The "winner" of a conflict was defined as the individual who has received a chatter vocalization, whereas the "loser" was defined as the individual who has exhibited a chatter vocalization.

Information on reproductive maturity, reproductive years, and the season, period, and context in which conflicts took place were available for all relevant agonistic encounters (Table 1). Using an average birth date of September 1 and assuming an average time to weaning of approximately 5 months (Richard, 1976) and gestation length of 5 to 6 months (Meyers and Wright, 1993), December and January were designated as the mid/late lactation period and February and March were designated as the mating season. Body mass measurements where both female and male body mass had been documented during the same calendar year of the encounter were available for 483 encounters. Outside of the late dry season, females and males experience similar seasonal fluctuations in body mass (Richard et al., 2000; Lewis and Kappeler, 2005), and differences in body mass are thus expected to remain approximately similar throughout the year. Because pregnant and non-pregnant females exhibit no significant difference in body mass (Lewis and Kappeler, 2005), pregnancy likely did not impact mass measurements.

Data Analysis

Generalized linear mixed models (GLMMs) were used to investigate factors influencing conflict outcome (win/loss) between females and males. Fixed factors included female reproductive maturity (mature/immature), reproductive year (yes/no), season (mating/non-mating), period (mid/late lactation/other), feeding context (feeding/non-feeding), and body mass difference (female body mass minus male body mass). The full dataset was used to test the influence of reproductive maturity and body mass. The influence of body mass differences was also tested separately in immature females alone to assess whether the body mass was more influential in the absence of reproductive maturity. To test the influence of reproductive year, I ran a reduced model that only included conflicts in which females were reproductively mature. Models testing the effect of mating season were further limited to both females and males that were reproductively mature, and reproductive period and context were examined only for females in reproductive years. Individual female and male ID were included as random factors for all models.

When applicable, variance inflation factors (VIFs) were computed for a joint model including all predictors to assess multi-collinearity prior to building models. Variables with VIFs greater than 5 were considered to reflect dependencies between included factors and were excluded from the model (Zuur et al., 2009; Rogerson, 2010). GLMMs were calculated using R package lme4 (Bates et al., 2014). Models were evaluated via AIC values to determine which combination of factors provided the most parsimonious explanation for conflict outcomes. Least-squares means from R package lsmeans were used to calculate predicted probabilities of conflict outcomes (Lenth, 2016). A repeated measures ANOVA was used to examine body mass differences

between adult females and males while accounting for repeated measures on individuals. All statistical analyses were conducted in R version 3.3.2 (R Core Team, 2016).

RESULTS

Intersexual Conflict and Reproductive Maturity

A total of 1,364 decided intersexual agonistic interactions occurred between 115 unique dyads ($N_{Female} = 31$, $N_{Male} = 33$). Overall, females won 81.3% of these interactions, with reproductively immature females winning 27.7% (76 out of 274 conflicts) and mature females winning 94.8% (1,033 out of 1,090 conflicts). Females were significantly more likely to win intersexual conflicts after reaching reproductive maturity ($p < 0.001$, Table 2). The predicted probability of an immature female winning an intersexual conflict was 32.70 $\pm$ 18.50% (mean $\pm$ SE) while the predicted probability of a mature female winning an intersexual conflict was 98.40 $\pm$ 1.56% (mean $\pm$ SE) (Figure 1).

Reproductive and Social Contexts

Neither reproductive year, reproductive period, nor feeding context had a significant influence on the probability of mature females winning intersexual conflicts (Table 2). While the majority of conflicts (57.80%) took place during a feeding context among reproductively mature females, context had no effect on the likelihood of females winning during mid/late lactation periods ($p = 0.22$, Table 2). However, mature females exhibited a tendency toward an increased likelihood of winning intersexual conflicts against mature males during the mating season ($p = 0.063$, Table 2).

Body Mass

Adult females and males exhibited no significant difference in average body mass ($N_{Females}$ = 12, mean = 3.15 $\pm$ 0.21 kg; N_{Males} = 27 , mean = 3.12 $\pm$ 0.31 kg; ANOVA: χ^2 = 0.28, df = 1, p = 0.60). However, both reproductively mature (p = 0.031) and immature females (p = 0.013) were significantly larger than male conflict partners (Table 2), with mature females most often approximately 0.20 $\pm$ 0.48 kg larger and immature females most often approximately 0.22 $\pm$ 0.60 kg larger than males. Body mass differences did not have a significant effect on the likelihood of females winning intersexual conflicts for females overall (p = 0.17) or for immature females (p = 0.21) (Table 2).

DISCUSSION

This study aimed to examine variables influencing the expression of female power in a Verreaux's sifaka population in Kirindy Mitea National Park through an investigation of the energy conservation (ECH), cost-asymmetry (CAH), and leverage (LH) hypotheses. Consistent with all three hypotheses, females win more intersexual conflicts after reaching reproductive maturity, and consistent with the LH, females exhibited a tendency to win more conflicts during the mating season. Contrary to the ECH and CAH, however, neither context nor energetically expensive periods predicted conflict outcome. Furthermore, body mass did not appear to influence conflict outcomes even when significant body mass differences between conflict partners were present, contrary to the CAH and LH. While none of the hypotheses were fully supported, results suggest that the expression of female-biased power in Verreaux's sifaka is best explained by factors associated with reproductive maturity and female leverage.

The Energy Conservation Hypothesis

The predictions of the ECH were only partially supported. Females were significantly more likely to win intersexual conflicts against males after reaching reproductive maturity, but were not significantly more likely to win during reproductive years or mid/late lactation periods. Furthermore, although female Verreaux's sifaka have a significantly higher energy intake during lactation periods (Koch et al., 2017), females in this study were equally likely to win intersexual conflicts between feeding and non-feeding contexts. In gray mouse lemurs (Hohenbrink et al., 2016) and ringtailed lemurs (Pereira, 2002; Cavigelli et al., 2003), the likelihood of females winning intersexual

conflicts is similarly associated with reproductive maturity, but not social or reproductive contexts.

My findings call into question the underlying assumption that female lemur energetic needs associated with reproduction are sufficient to require consistent expression of female power over males. Indeed, interspecific comparisons of postnatal investment costs show no significant differences between lemurs and other closely related taxa (Tilden and Oftedal, 1995; Kappeler, 1996; Tilden and Oftedal, 1997). Alternatively, female lemur energy needs may be higher than males' regardless of reproductive context. The Verreaux's sifaka gestational period coincides with the period of lowest food availability, and females lose significantly more body fat than males during this time (Lewis and Kappeler, 2005). Thus, while lactation periods may still be the most energetically costly for females overall (Emery Thompson, 2017), the breeding strategy employed by Verreaux's sifaka may increase female energy needs relative to males' even outside of these periods. Additional measures of energy metabolism in female and male lemurs during different reproductive stages are necessary before drawing any definitive conclusions, however (Kappeler and Fichtel, 2015).

The Cost Asymmetry Hypothesis

The Kirindy Mitea Verreaux's sifaka population exhibited no significant difference in body mass among adult females and males at the population level, consistent with the reported monomorphism in other populations (Ravosa et al., 1993; Richard et al., 2002; but see Lewis and Kappeler, 2005). However, significant differences in body mass existed between conflict partners, where females were significantly larger

than males even when females were reproductively immature. Despite these differences, body mass had no significant effect on conflict outcome.

These results may suggest that body mass is an inadequate proxy for fighting ability in Verreaux's sifaka. Agonistic interactions in many arboreal species, including Verreaux's sifaka, depend upon charges and chases rather than physical conflicts (Kappeler, 1990), suggesting a minimal role for body size. Differences in fighting ability may thus be more accurately represented by morphological factors associated with speed and agility (Clutton-Brock, 1977; Clutton-Brock, 1985; Kappeler, 1990; Plavcan and Van Schaik, 1997), such as leg shape (Lawler et al., 2005).

Alternatively, body mass differences simply may not have been large enough to reflect any real differences in fighting ability. Indeed, while many vertebrate taxa demonstrate a positive correlation between body size and dominance, this relationship often disappears when size differences are small (Chase and Seitz, 2011). In fish, for example, size differences above 20% are associated with increasing dominance rank, while size differences below 10% have no effect (Beaugrand et al., 1996). Other species with intersexual body size differences below 10% similarly fail to exhibit any association between dominance and body size (e.g., grey squirrels: Allen and Aspey, 1986; yellow-pine chipmunks: Schulte-Hostedde and Millar, 2002). Given that intersexual mass differences in Kirindy Mitea Verreaux's sifaka differed by only about 0.20 kg, which represents at most about 13% of the total body mass in the immature individuals included in this study, a similar explanation may apply.

Thus, while my findings do not support the predictions of the CAH that pertain to body mass specifically, they may support the underlying premise that female dominance is dependent upon female and male fighting abilities being approximately equal (Dunham, 2008). Before definitively supporting this conclusion, however, methodological issues must also be taken into account. Mass differences between females and males were assumed to remain approximately the same for the entire year despite known variability during the late dry season (Richard et al., 2000; Lewis and Kappeler, 2005) and rapid growth during infant, juvenile, and subadult development (Ravosa et al., 1993). However, given that studies involving more consistent measures of body mass have demonstrated insignificant effects of body mass on intersexual conflict outcome in species with female-biased power structures (Hohenbrink et al., 2016), the results of the present study may still accurately reflect the influence of body mass regardless of the number of mass data points used.

The Leverage Hypothesis

Verreaux's sifaka exhibited a tendency toward an increase in the probability of females winning intersexual conflicts during the mating season, which is consistent with findings in several other species suggesting that mating opportunities present a source of leverage. Females in species characterized by female-biased power structures, for example, have been found to exhibit an increased likelihood of winning intersexual conflicts during estrus (e.g., bonobos: Surbeck and Hohmann, 2013) or during

reproductive periods in general (e.g., gray mouse lemurs, Goodman's mouse lemurs: Hohenbrink et al., 2016). Even females in species characterized by male-biased power structures and male-biased size dimorphism may gain short-term advantages over males as a result of leverage derived from mating opportunities (e.g., eastern lowland gorillas: Sicotte, 2002; orangutans: van Noordwijk and van Schaik, 2009). Given that females and males exhibited minimal differences in body mass, the results of the present study are thus consistent with the leverage hypothesis, suggesting that female power in Verreaux's sifaka is primarily moderated by female leverage rather than female fighting abilities.

These results should be considered with caution, however. While February and March were designated as the mating season, mating bouts usually only take place within a six-week period within January and March (Brockman et al., 1999; Leimberger and Lewis, 2017) and females are in estrus for a maximum of three days within this period (Brockman et al., 1999). Without any hormonal data to accurately assess when estrus occurred and rare observations of copulations (Lewis, *unpublished data*), assessing whether the increase in female wins is truly influenced by leverage via mating opportunities is difficult. Furthermore, these results may have also been confounded by kinship, which has been shown to influence agonistic interactions in other lemur species (Kappeler, 1993b). If females were primarily interacting with male kin during the mating season, the increase in the likelihood of mature females winning intersexual conflicts found in this study would likely be unrelated to leverage as mating opportunities, and instead may reflect leverage as kinship (Hand, 1986; de Waal, 1986). Future research

incorporating kinship and hormonal data are necessary to further delineate how leverage affects the expression of female-biased power structures in Verreaux's sifaka.

Reproductive Maturity and Female-Biased Power Structures

The hypotheses tested in this study are unified by the common expectation that female-biased power is established only after females reach reproductive maturity. This prediction was clearly supported by the results of this study as well as others investigating the establishment of female-biased power (Pereira, 2002; Cavigelli et al., 2003; Hohenbrink et al., 2016). Intersexual power relationships within male-biased power structures are also influenced by reproductive maturity (Holekamp and Smale, 1991), suggesting that this period has implications for the development of intersexual power asymmetries more generally.

Reproductive maturity is accompanied by a myriad of individual changes reflecting the differential reproductive strategies employed by females and males as a result of specific limitations constraining female versus male reproductive success (Trivers, 1972). While these limitations are not necessarily correlated with any one specific reproductive strategy (Clutton-Brock, 2007), they nevertheless involve differences in factors such as energy requirements, body size, hormone levels, and new sources of economic power, such as mating opportunities (Holekamp and Smale, 1991; Pereira, 1995; Plant and Barker-Gibb, 2004; Emery Thompson, 2017). Intersexual power asymmetries that form after reaching reproductive maturity thus do not necessarily reflect

reproductive maturity itself, but instead reflect changes in the variables involved in and/or produced from reaching this developmental stage.

While consistent asymmetries in intersexual relationships ultimately arise from the combined interactions of these variables (Lewis, *in press*), some factors may nevertheless prove to be more influential than others. In species characterized by female-biased power structures and minimal body size differences between sexes, such as Verreaux's sifaka and other lemurs, the present study suggests that mating opportunities as a source of female leverage may be particularly influential, although the relative insignificance of body mass differences and energy requirements are equally important to consider. Because male reproductive success usually depends more on access to mates than does female success (Trivers, 1972), mating opportunities may thus be considered of higher value to males relative to females. Females can then exploit this asymmetry by controlling access to this resource, and mating opportunities may thus become a source of female leverage (Lewis, 2002). However, because mating opportunities only occur within particular time periods, use of this form of leverage may not result in consistent female-biased power if males hold alternative sources of power, such as larger body size, outside of these time periods (Lewis, 2002). Female-biased power structures driven by female leverage may thus depend upon relative equality between females and males in all other sources of power. Given that only one other study has examined female leverage in relation to female-biased power (Surbeck and Hohmann, 2013), however, and no other studies have done so in a monomorphic species, additional research is essential to test the validity of this claim.

CONCLUSIONS

The expression of female-biased power in Verreaux's sifaka at Kirindy Mitea National Park is influenced by factors associated with reproductive maturity and female leverage. Neither body mass differences nor any other reproductive or social contexts had any influence on the likelihood of females winning intersexual conflicts. However, body mass differences may not have been large enough to reflect differences in fighting ability. Thus, the leverage hypothesis, but not the energy conservation nor cost-asymmetry hypothesis, was fully supported by the results of this study. Future research should consider incorporating physiological measures of female energetics and reproductive stages as well as sources of fighting ability other than body mass before these hypotheses are completely discounted, however.

Table 1. Definitions of key variables used to determine the factors that may be most influential in mediating the expression of female-biased power in Verreaux's sifaka.

Variable	Definition
Win	Submissive signal is received (provoked or unprovoked by aggression).
Female reproductive maturity	Age at first observed birth.
Reproductive year	Year in which female gave birth to infant that survived to weaning age. Females with infants that died prior to weaning were excluded from analyses.
Mating season	Assuming a birth date of September 1st and gestation length of approximately 5 to 6 months, February and March were designated as the mating season.
Mid/late lactation	Assuming a birth date of September 1st and weaning at 5 months, December and January were designated as the mid/late lactation period.
Feeding context	Conflicts occurring in food trees and during feeding and foraging bouts.

Table 2. Table of results from generalized linear mixed effects models. Behavioral and morphological data collected from Verreaux's sifaka at Kirindy Mita National Park from 2007-2016 were used to test the influence of i) reproductive maturity, ii) body mass differences, iii) various reproductive contexts and iv) the feeding context on the likelihood of females winning intersexual conflicts.

	Estimate	SE	*p* value
Model 1. **Win ~ Reproductive Maturity + Body Mass Difference (All Females)**			
Intercept	-1.70	1.37	0.22
Reproductive Maturity	7.62	1.99	**<0.001**
Body Mass Difference	0.88	0.65	0.17
Model 2. **Win ~ Body Mass Difference (Immature Females)**			
Intercept	-3.44	3.20	0.28
Body Mass Difference	1.90	1.52	0.21
Model 3. **Win ~ Reproductive Year**			
Intercept	31.37	57.48	0.59
Reproductive Year	-24.87	57.47	0.67
Model 4. **Win ~ Reproductive Season**			
Intercept	6.04	1.70	<0.001
Mating Season	1.41	0.76	**0.063**
Model 5. **Win ~ Reproductive Period**			
Intercept	6.09	2.17	0.0051
Mid/Late-Lactation Period	0.57	0.87	0.52
Model 6. **Win ~ Context**			
Intercept	8.91	0.0040	<0.001
Feeding Context	1.96	1.58	0.22

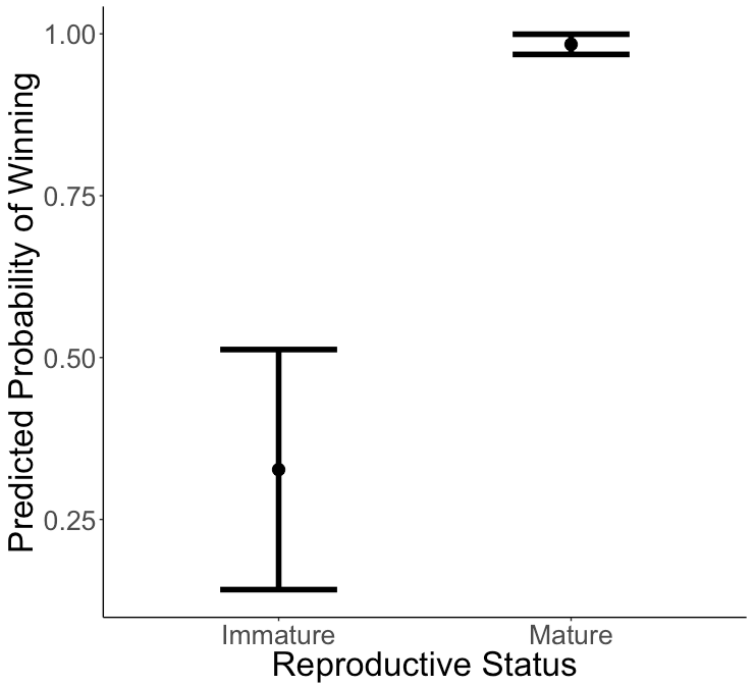

Figure 1. Reproductively mature females are significantly more likely to win intersexual conflicts that immature females. The least-squares predicted mean probabilities ± standard errors of female winning an intersexual conflict when reproductively immature vs. mature are displayed.

Chapter 2. Monomorphism in mammals: A review of current hypotheses

INTRODUCTION

Sexual dimorphism is defined as the morphological differentiation of sexually mature females and males (Fairbairn, 1997), with sexual size dimorphism specifically referring to intersexual differences in body size. Among mammals, male-biased size dimorphism is commonly assumed to be predominant, with extreme examples of male-biased dimorphism in orders Primates and Carnivora (Ralls, 1976; Andersson, 1994; Fairbairn, 1997; Weckerly, 1998; Lindenfors et al., 2007). Despite this overarching trend, however, several mammalian species exhibit sexual size monomorphism, where female and male body sizes are approximately equal.

While numerous studies have examined sexual size dimorphism in mammals and the potential pressures selecting for different body sizes (Ralls, 1976; Weckerly, 1998; Isaac, 2005; Lindenfors et al., 2007; Plavcan, 2011), mammalian sexual size monomorphism has not yet been reviewed. In part, the lack of broad-scale studies examining monomorphism may be related to the assumption that monomorphism exists only as a product of phylogenetic inertia (Cheverud et al., 1985; van Schaik and Kappeler, 1996; Pérez-Barbería et al., 2002). However, this justification does nothing to explain the forces responsible for the original development of monomorphism nor its continued expression in extant species (Kappeler, 1990; Lindenfors and Tullberg, 1998). This review aims to address these issues by examining the extent of size monomorphism among mammals and review the existing hypotheses to put forward to explain this morphological pattern.

Definitions

Primary sex differences refer to gonadal sexual differentiation and relate directly to mating and reproduction, whereas secondary sex differences refer to other traits that distinguish between the sexes (vom Saal, 1989; Andersson, 1994; Plavcan, 2001). While monomorphic and dimorphic traits can refer either to primary and secondary sex characteristics, discussions surrounding sexual monomorphism or dimorphism generally refer only to differences in secondary sex characteristics (Plavcan, 2001). In mammalian species, secondary sex characteristics such as body and/or weaponry size (e.g., canines, horns, antlers) are most often used to determine the degree of dimorphism or monomorphism.

Because body size applies to all species (as opposed to weaponry, which is usually limited to specific taxonomic groups), it is the most common measure used when comparing intersexual differences across taxonomic groups (Ralls, 1977; Fairbairn, 2007; Fairbairn, 2013). Body size in extant mammals is usually represented by total body mass, although skeletal measurements may also be used (Ralls, 1976; Schmidt-Nielson, 1984; Andersson, 1994; Weckerly, 1998; Fairbairn, 2007). Both measurements have limitations in their accuracy. Body mass may be influenced by seasonal fluctuations, hydration, or food consumption, leading to poor repeatability among individuals (Fairbairn, 2007). In contrast, skeletal measurements have better repeatability, but often underestimate variance in body size (Fairbairn, 2007). Despite these limitations, body mass is generally accepted as the standard measure for body size because it gives a more direct measure of three-dimensional size (Schmidt-Nielson, 1984; Weckerly, 1998). This review therefore focuses primarily on body mass monomorphism and references to monomorphism or dimorphism herein refer to sexual size monomorphism or dimorphism.

A species is usually considered monomorphic when body mass differs by less than 10% between sexes (Weckerly, 1998; Lindenfors et al., 2007; Dunham and Rudolf, 2009), although this cut-off is not necessarily regarded as a standard across the literature. Some studies, for example, refer to a 10% or less difference in body size as moderate sexual size dimorphism, while others give no indication as to where the cutoff for monomorphism or dimorphism lies (Ralls, 1976; Fairbairn, 2007). Unfortunately, the only known study to investigate the validity of this threshold limited their assessment to monomorphism and male-biased dimorphism, classifying species in which females are larger than males as monomorphic (Pérez-Barbería and Gordon, 2002) and thereby potentially biasing their results. Additional research is clearly necessary to determine whether the 10% cutoff is appropriate, but for the purposes of this review, references to monomorphism can be assumed to be defined by this measure unless otherwise noted.

Monomorphism in Mammals

While the prevalence of monomorphism has not been assessed directly in mammals, a general understanding may be attained by first examining the prevalence of female- and male-biased dimorphism. Female-biased dimorphism, despite characterizing most animal species, appears to be relatively uncommon in mammals (Fairbairn, 2013). Based on species-level analyses of both limb measurements and body weight, Ralls (1976) reported that 60% of mammalian orders exhibit female-biased dimorphism, but in most of these orders the degree of dimorphism was slight, with females less than 10% larger than males. Under the most commonly used definition of monomorphism, those orders thus exhibit monomorphism rather than dimorphism (Weckerly, 1998; Lindenfors et al., 2007; Dunham and Rudolf, 2009; but see Ralls, 1976). More recent analyses

specifically examining body mass dimorphism support these results, showing that only one order (Lagomorpha) exhibits significant female-biased dimorphism (Lindenfors et al., 2007).

In contrast, male-biased dimorphism is commonly assumed to be the prevailing pattern in mammals (Ralls, 1977; Alexander et al., 1979; Weckerly 1998; Pérez-Barbería et al., 2002; Lindenfors et al., 2007; Fairbairn, 2013) and has been the focus of most broad-scale studies examining female and male body size in various mammal taxa (e.g., Leutenegger and Cheverud, 1982; Weckerly, 1998; Plavcan, 2001; Isaac, 2005). The most comprehensive study of dimorphism in mammals to date included an assessment of body-mass measurements for almost 30% of known mammals and showed that for mammals overall, male body mass exceeds female body mass by approximately 18% on average (Lindenfors et al., 2007). In male-biased dimorphic orders for which enough data was available to achieve statistical significance (8 out of 26), male body mass averaged 25% to 90% greater than female body mass. These findings are supported by smaller-scale studies of male-biased dimorphism in orders Primates (Plavcan, 2001; Weckerly, 1998), Artiodactyla (Weckerly, 1998; Pérez-Barbería and Gordon, 2000), and Carnivora (Moors, 1980; Weckerly, 1998), among others.

However, the predominance of male-biased dimorphism in mammals may be overestimated. By determining the extent of dimorphism in terms of average intersexual size differences rather than determining the proportion of species exhibiting these intersexual body size patterns, extreme values of dimorphism within a few taxonomic groups can easily skew results (Martin et al., 1994). Among primates, for instance, the degree of male-biased dimorphism is largely influenced by catarrhines, with males sometimes more than twice the size of females, while platyrrhines are characterized by lesser degrees of male-biased dimorphism (22% on average) and strepsirrhines are

primarily monomorphic (Kappeler, 1990; Martin et al., 1994; Weckerly, 1998; Plavcan, 2001; Dunham et al., 2009). Family Phocidae provides a more extreme example, in which male body mass averages 81% larger than female body mass, but males are more than 10% larger than females in only 47% of species studied (Weckerly, 1998). Indeed, species-level analyses examining male-biased dimorphism in mammals overall show that males are more than 10% larger than females in less than half of all mammals (Lindenfors et al., 2007). Combined with a small proportion of species exhibiting significant female-biased dimorphism (Ralls, 1976), these results suggest that monomorphism may be more prevalent in mammals than has been historically represented in the literature.

This overemphasis of male-biased dimorphism has biased the hypotheses put forward to explain intersexual differences in body size. Indeed, hypotheses addressing monomorphism in mammals must often be inferred from hypotheses explaining male-biased dimorphism (e.g., Clutton-Brock, 1977; Andersson, 1994; Plavcan, 2001), and the few hypotheses that address monomorphism specifically are limited to particular taxonomic groups (e.g., Kappeler, 1990; Pérez-Barbería et al., 2002; Dunham and Rudolf, 2009; Dunham et al., 2013). Primates, for example, are often used as a model taxon for better understanding patterns of intersexual body size differences, perhaps due to the high levels of variation in the intersexual body size differences exhibited by primate species (Clutton-Brock, 1977; Ralls, 1977; Dunham et al., 2013). Most hypotheses explaining monomorphism are thus drawn from primate species (e.g., Kappeler, 1990; van Schaik and Kappeler, 1996; Wright, 1999; Dunham and Rudolf, 2009). Among the most common explanations (not mutually exclusive) are that monomorphism is a result of either non-adaptive processes, such as phylogenetic inertia (van Schaik and Kappeler, 1996; Pérez-Barbería et al., 2002) or allometric trends

(Leutenegger and Cheverurd, 1982), or adaptive processes related to natural (Wright, 1999) or sexual selection (Plavcan, 2001).

NON-ADAPTIVE HYPOTHESES

Allometric Trends

Rensch's rule, a non-adaptive explanation for monomorphism (Leutenegger and Cheverurd, 1982), describes the general tendency of sexual size dimorphism to increase with mean body size in clades where males are larger, and decrease with mean body size in clades where females are larger (Rensch, 1960; Abouheif and Fairbairn, 1997). This covariation between body size and dimorphism is suggested to result from sexual selection (Székely et al., 2004; Dale et al., 2007), where directional sexual selection acting on one sex is predicted to produce a correlated but weaker change in the other sex (Abouheif and Fairbairn, 1997; Fairbairn, 1997).

Empirical support for this trend is equivocal, however. On broad scales (e.g., among animal classes), Rensch's rule is supported only in cases where males are the larger sex (Ralls, 1977; Abouheif and Fairbairn 1997; Fairbairn 1997; Weckerly, 1998; Lindenfors et al., 2007). Within mammals as a class, for example, a slight but significant relationship exists between body size and dimorphism, with monomorphic mammals exhibiting a tendency towards overall smaller body sizes (Weckerly, 1998; Lindenfors et al., 2007). Across mammalian orders, however, Rensch's rule is only supported in orders Primates and Diprotodontia (Lindenfors et al., 2007; Sibly et al., 2012), although even within primates, neither strepsirrhines nor platyrrhines follow Rensch's rule and results are contradictory in catarrhines (Clutton-Brock et al., 1977; Leutenegger and Cheverud, 1985; Kappeler, 1990; Martin et al., 1994; Abouheif and Fairbairn, 1997; Lindenfors and

Tullberg, 1998; Weckerly, 1998; Smith and Cheverud, 2002; Gordon, 2006). Additional studies at narrower taxonomic levels similarly show a lack of support for Rensch's rule, including pinnipeds (Lindenfors et al., 2002), ungulates (Berger and Gompper, 1999; Polak and Frynta, 2009), rodents (Martínez and Bidau, 2016), bats (Stevens and Platt, 2014), felids (Martínez et al., 2014), and canids (Bidau and Martínez, 2016). As with other ecological rules, these exceptions demonstrate that Rensch's rule may outlines general patterns, but cannot be used as an absolute ecological law (Sibly et al., 2012).

Phylogenetic Inertia

Most animals exhibit little to no differences in body size between females and males, with females and males typically differing by only 5 to 10 percent (Fairbairn, 2013), including mammals (Lindenfors et al., 2007). As a result, monomorphism may simply be the result of phylogenetic inertia (Cheverud et al., 1985; van Schaik and Kappeler, 1996; Pérez-Barbería et al., 2002), which attributes the persistence of non-adaptive characteristics to the retention of ancestral traits adapted during different conditions (Martin et al., 1994; Shanahan, 2011), and therefore may simply exist as the default condition in mammals. Indeed, monomorphism was likely the ancestral condition of most ungulate species (Pérez-Barbería et al., 2002). Similarly, when comparing the influence of phylogeny with that of body mass, mating system, habitat, and diet, phylogenetic effects were found to explain 50% of the variation in dimorphism in primates (Cheverud et al., 1985; but see Kappeler, 1990). Regardless of whether monomorphism currently exists only as a remnant ancestral trait, however, this explanation ultimately does not address the causes responsible for its original development (Kappeler, 1990; Lindenfors and Tullberg, 1998).

ADAPTIVE HYPOTHESES

Sexual Selection Hypotheses

The adaptive evolution of intersexual size differences (including monomorphism, male-biased dimorphism, and female-biased dimorphism) is predominantly explained by sexual selection (Darwin, 1871; Leutenegger and Kelly, 1977; Kappeler, 1990; Martin et al., 1994; Leigh and Shea, 1995; Plavcan, 2001; Lindenfors et al., 2002; Isaac, 2005; Gordon, 2006; Dale et al., 2007; Lindenfors et al., 2007; Cox and Calsbeek, 2009; Plavcan, 2011). Sexual selection theory is traditionally based on the premise that females tend to engage in mate choice whereas males tend to engage in competition for mates (Plavcan, 2001; Kokko and Jennions, 2008; Plavcan, 2011). Combined, these forces lead to sex-specific effects on males (Ralls, 1977; Andersson, 1994; Plavcan, 2001; Plavcan, 2011). While modern assessments of sexual selection recognize that mate choice and competition are not always exclusive to one sex (Gowaty and Hubbell, 2005), most hypotheses regarding intersexual size differences focus on male competition alone, with particular emphasis on positive sexual selection for male body size (Andersson, 1994; Plavcan, 2001). These hypotheses predict that monomorphism occurs when (1) males cannot monopolize females due to spatial or temporal female dispersal (2) male-male contest competition for mates is weak, and (3) male reproductive variation is low, with the latter two predictions often discussed in terms of mating systems (Emlen and Origin, 1977; Kleiman, 1977; Andersson, 1994; Plavcan, 2001). In the case that these predictions are not supported, monomorphism is predicted when male intrasexual competition depends on traits other than body size (i.e., when positive sexual selection for male body size is weak: Lawler, 2005; Dunham and Rudolf, 2009) or when females exhibit a preference for smaller, more compliant males (Richard, 1992).

Female Aggregation

Female temporal and spatial aggregation is in part determined by habitat type and predation (Andersson 1994; Caudron, 1997; Plavcan, 2001; Peréz-Barbería, 2002). These factors may determine the low levels of female aggregation found in monomorphic pack-ice breeders and arboreal mammals (Jarman, 1974; Ralls, 1977; Le Boeuf, 1986; Andersson, 1994; Plavcan and van Schaik, 1997; Plavcan 2001). In response to the instability of pack ice, for example, many seals have adapted near-synchronous birthing followed soon thereafter by synchronized, short female receptivity periods (Ralls, 1977; Le Boeuf, 1986; Andersson, 1994). Furthermore, females are often more widely dispersed on pack ice than land or land-fast ice (i.e., ice attached to a land mass), possibly due to dispersed food resources (Ralls, 1977; Le Boeuf, 1986). As a result, the pack ice breeding habitat effectively inhibits males from monopolizing females through both temporal and spatial dispersal of females. Arboreal or closed habitats may also inhibit large aggregations of females, either through widely dispersed food resources or cryptic anti-predator behaviors (Jarman, 1974; Ralls, 1977; Plavcan and van Schaik, 1997; Plavcan 2001). Ungulates became dimorphic only after moving into open habitats and forming large female groups, whereas previously closed-habitat species were monomorphic with dispersed females (Peréz-Barbería et al., 2002).

Mating Systems

Mating systems are often used as a proxy to infer the degree of sexual selection on male body size (e.g., Plavcan, 2000; Sibly et al., 2012; Cullen et al., 2014). This explanation relies on the assumption that monogamy and polygynandry are characterized by little to no positive sexual selection on male body size (thus leading to monomorphism

or female-biased dimorphism), whereas polygyny is characterized by strong positive selection on male body size (thus leading to male-biased dimorphism) (Kleiman, 1977; Jarman, 1983; Boonstra et al., 1993; Cullen et al., 2014). The strength of sexual selection on males is often quantified using male reproductive variance as a proxy, where high reproductive skew represents strong sexual selection and vice versa (Isaac, 2005).

Support for this relationship is mixed, however. A correlation between mating system and body size has been demonstrated in primates (Clutton-Brock, 1977; Leutenegger and Kelly, 1977; Martin et al., 1994; Mitani et al., 1996; Weckerly, 1998; Plavcan, 2000), ungulates (Peréz-Barbería, 2002; Koren et al., 2006; Cooper et al., 2011; Bar Ziv et al., 2016), pinnipeds (Le Boeuf, 1986; Lindenfors et al., 2002; Cullen et al., 2014), and both bovids and cervids (Jarman 1983, Sibly et al. 2012). However, no such support has been found in perissodactyls (Berger and Cunningham, 1994; Garnier et al., 2001) or rodents (Boonstra et al., 1993; King and Allainé, 2002; Isaac, 2005). In fact, monogamy is relatively rare in rodents despite widespread monomorphism, a notable trend given that rodents comprise 44% of all mammals (Wolff, 2007). In primates, removing monogamous species from analyses effectively eliminates the relationship between dimorphism and polygyny (Clutton-Brock, 1977; Martin et al. 1994), while studies of voles have found no relationship at all between intersexual size differences and mating systems (Hesk and Ostfeld, 1990). Additionally, only 3% of all mammals are reported as monogamous (Kleiman, 1977), but substantially more than 3% of species are monomorphic.

These contradictory results may be related to the methods used to define the mating system. Traditionally, mating systems have been defined by mating success, but this measure does not always correlate with reproductive success (Isaac, 2005). Indeed, studies utilizing genetics-based paternity analyses to quantify male reproductive success

show that variation is relatively low in many monomorphic species with polygynous mating systems, including roe deer (Vanpe et al., 2007), muriquis (Strier, 1990; Strier et al., 2011), collared peccaries (Packard et al., 1991; Cooper et al., 2011), and harbor seals (Coltman et al., 1999). Because sexual selection ultimately depends upon variation in reproductive success, future studies examining intersexual size differences and mating systems may benefit from distinguishing between mating and reproductive success.

Monomorphism has also been found in polygynous species with high reproductive skew, however. Perhaps some of the best characterized examples of monomorphic species with highly polygynous mating systems (as defined by reproductive success) can be found among lemurs, which include some of the most unambiguously monomorphic species among all mammals and demonstrate no correlation between intersexual size differences and mating system (Kappeler, 1990; Kappeler and Ganzhorn, 1993; Weckerly, 1998). While male-male contest competition can be fierce, particularly during the mating season, these agonistic interactions consist primarily of charges and chases rather than physical conflicts (Kappeler, 1990). Regardless, sexual selection is still strong in many species, as evidenced by high reproductive skew among males (Lawler et al., 2005; Kappeler, 2008; Parga et al., 2016). In this case, sexual selection on male body size is likely weak and may instead act upon male traits such as speed and agility (Clutton-Brock, 1977; Clutton-Brock, 1985; Kappeler, 1990; Plavcan and Van Schaik, 1997; Lawler, 2005). In sifaka, directional selection acts on leg shapes beneficial for vertical clinging and leaping locomotion, while stabilizing selection acts on body size (Lawler, 2005). Similar suggestions regarding selection for speed and agility have been made for monomorphic, polygynous marine mammals, but support is limited (Andersson, 1994).

Female Choice

Few studies have explicitly examined the role of female choice in the development and maintenance of monomorphism (Richard, 1992; Leigh and Terranova, 1997; Lawler et al. 2005; Plavcan 2011), an extreme oversight given that sexual selection is dependent on both females and males. The few hypotheses that have been presented are derived from studies of female-dominant lemur species, and suggest that male reproductive success in these species is determined by competitive submission to females rather than competitive aggression between males (Richard, 1992). Because small males will not challenge females or infants for food (Jolly, 1984), female preference for compliant males may provide selection against large male body size and thus allow for monomorphism (Richard, 1992). Empirical tests of this hypothesis have yet to be conducted, however.

In species where females mate with multiple males, cryptic female choice may also play a role in maintaining monomorphism. This form of mate choice refers to the anatomical and physiological characteristics of females that favor corresponding traits in males (Parker et al., 2013). Theoretical models predict a trade-off between traits subject to female choice pre- and post-copulation, such that males must modulate investments between traits that aid in mate acquisition, such as body size, and traits that aid in fertilization success (Parker et al., 2013; Lüpold et al., 2014). For species in which males invest more in post-copulatory traits to ensure fertilization success, selection pressure on male body size is expected to be alleviated, thus providing a possible explanation for monomorphism (García-Navas, 2017). Support for this hypothesis in mammals has been empirically demonstrated in primates (Dunham and Rudolf, 2009) and rodents (García-Navas, 2017), although testing in ungulates demonstrated a lack of support (Ferrándiz-Rovira et al., 2014).

Passive mate guarding is one such post-copulatory trait that involves both cryptic female choice and male-male competition (i.e., sperm competition). While contest competition is primarily thought to occur via active mate guarding, where post-copulatory males actively defend their mating partners against other males, passive mate guarding is expected when males are unable to feasibly monopolize mating access to all females, such as in species with short female sexual receptivity lengths (e.g. less than 4 days) or in species with dispersed social systems, given that males may not be present to defend mating partners (Dixson and Anderson, 2002; Dunham and Rudolf, 2009). This strategy involves the use of copulatory plugs, where semen solidifies and molds to the female vaginal canal after ejaculation (Voss, 1979; Dixson and Anderson, 2002; Dunham and Rudolf, 2009). In primates, a clear association exists between copulatory plugs and body size, with copulatory plugs employed almost exclusively by monomorphic species (Dunham and Rudolf, 2009). Orders Rodentia, Chiroptera, and Eulipotyphla are also characterized by monomorphism (Lindenfors et al., 2007) and appear to exhibit widespread use of copulatory plugs (Engle, 1926; Voss, 1979), although a relationship between body size and passive mate guarding has yet to be demonstrated empirically in these groups.

NATURAL SELECTION HYPOTHESES

While sexual selection is generally considered the strongest force in determining intersexual body size differences (Cox and Calsbeek, 2009), it is unlikely to be the only force in operation (Isaac, 2005). Natural selection is thought to play a smaller, but still significant role in shaping female and male body size (Gordon, 2006). Natural selection hypotheses concerning monomorphism specifically suggest that similar female and male

body sizes result from constraints on body size related to environmental variables or habitat type (Plavcan, 2001; Tennenhouse, 2015). While tests of these hypotheses are considerably limited relative to sexual selection hypotheses, these forces may still play a role in selecting for monomorphism.

Environmental Constraints

Environmental constraints, including extreme environmental variability, seasonality, and resource unpredictability, have long been cited as potential causal factors for monomorphism (Jolly, 1984; Leigh and Terranova, 1998; Weckerly, 1998; Wright, 1999; Plavcan, 2001; Dunham et al., 2013). Environmental constraints are hypothesized to impose a limit on male body size by acting against the prolongation of male growth (Leigh and Terranova, 1998; Wright 1999) and thereby limiting intersexual differences in growth duration or rate (Leigh and Shea, 1995; Leigh and Terranova, 1998). These constraints on intersexual bimaturism are predicted to occur when individuals must quickly reach a particular size and level of foraging competency so that they might survive during periods of low resource availability (Leigh and Terranova, 1998). Additionally, highly variable resource availability is predicted to increase female size through increased female-female contest competition for food resources (Jolly, 1984; Plavcan and van Schaik, 1997). The few studies that have tested these predictions, however, found no correlation between environmental constraints and intersexual body size differences (Dunham et al., 2013; Tennenhouse, 2015). Additional empirical data is necessary to determine whether a relationship between environmental constraints and monomorphism exists.

Habitat Type

Habitat type has been clearly shown to correspond with patterns of intersexual body size differences. Strictly arboreal species tend to be monomorphic, whereas terrestrial species tend to be male-biased dimorphic in both primates (Clutton-Brock et al., 1977; Leutenegger and Kelly, 1977; Cheverud et al., 1985; Martin et al., 1994; Plavcan and van Schaik, 1997; Plavcan, 2001) and rodents (Mace, 1979). This pattern may be due to selection based on constraints of arboreal locomotion (Leutenegger and Kelly, 1977; Plavcan and van Schaik, 1997) or food resources, which often occur on terminal branches (Clutton-Brock et al., 1977). Marine mammals also show variation in intersexual size differences that correspond to the degree of terrestriality, where species breeding on pack-ice tend to be monomorphic whereas terrestrial breeders tend to be male-biased dimorphic (Le Boeuf, 1986). Similarly, ungulates dwelling in "closed" habitats (i.e., forests, woodlands, bushlands, or thickets) tend to exhibit monomorphism whereas those dwelling in open terrain tend to exhibit male-biased dimorphism (Estes, 1974; Peréz-Barbería et al., 2002). Unlike arboreal species, however, the relationship between monomorphism and habitat in marine mammals and ungulates does not appear to be related to substrate-induced body size constraints, but is instead attributed to the degree of female aggregation (related to sexual selection) and vulnerability to predation (Ralls, 1977; Andersson, 1994).

Predator Defense Hypothesis

The predator defense hypothesis posits that in habitats with increased vulnerability to predation, natural selection for larger male body size is expected if males are primarily responsible for predation defense (DeVore and Washburn, 1963;

Leutenegger and Kelly, 1977; Martin et al., 1994). The corresponding prediction that monomorphism occurs in species living in habitats where predation levels are relatively low (Jarman, 1983; Anderson, 1986; Caudron, 1997) has received mixed support, and has only been tested in two taxa. In primates, there is a significant relationship between predation vulnerability and the degree of dimorphism (Anderson, 1986). In pack-ice breeding marine mammals, however, no such support exists (Le Boeuf, 1986; Caudron, 1997; Cassini, 1999). These species were actually found to undergo significant levels of predation, and some studies have suggested that weak predation may instead allow for increased dimorphism rather than monomorphism (Andersson, 1994; Cassini, 1999).

In the event that predation is high, the predator defense hypothesis provides additional predictions. Specifically, it predicts that alternative defense tactics are utilized that either a) do not depend on males alone, and/or b) do not depend on large body size (Jarman, 1983; Anderson, 1986; Caudron, 1997). This prediction has received considerably greater support relative to the first prediction. Monomorphic primate species (Leutenegger and Kelly, 1977) and marine mammals (Hammerschlag et al., 2006) tend to rely on predator detection and fleeing versus aggressive, size-dependent defense. Similarly, monomorphic ungulates dwelling in closed habitats also tend to utilize anti-predator behaviors unrelated to body size, primarily relying on crypsis or fleeing rather than active defense (Jarman 1974). For group-living mammals in general, monomorphism is suggested to lend to uniformity that may aid in confusing predators, making it difficult to single out an individual and further contributing the dilution effect (Leutenegger and Kelly, 1977; Jarman, 1983). Alternatively, males and females may contribute equally to predation defense, selecting for equally large body sizes in both sexes (Jarman, 1983).

CONCLUSIONS

Sexual size monomorphism in mammals is more common than typically presented in the literature (Lindenfors et al., 2007). Similar to hypotheses concerning the development and maintenance of sexual size dimorphism, hypotheses concerning monomorphism do not appear to have a clear unifying feature across all taxa (Weckerly, 1998). Of all hypotheses presented, however, factors relating to sexual selection appear to be most likely determinants. In terms of sexual selection overall, monomorphism is expected in species where selection for male body size is weak or is acting on traits unrelated body size, such as agility or genital morphology (Andersson, 1994; Plavcan, 2001; Isaac, 2005). Factors such as environmental constraints, habitat type, or predation pressure may contribute to sexual selection effects via female spatial or temporal dispersal (Le Boeuf, 1986; Caudron, 1997; Pavcan, 2001; Peréz-Barbería et al., 2002). Alternatively, habitat-related factors may place limitations on body size unrelated to sexual selection, leading instead to natural selection for smaller body sizes or greater agility (Clutton-Brock, 1977; Clutton-Brock, 1985; Kappeler, 1990; Andersson, 1994; Plavcan and Van Schaik, 1997; Lawler, 2005). Resolution of these broad-scale trends associated with monomorphism will require large-scale, species-level comparative work focused specifically on monomorphic species.

References

Abouheif E, Fairbairn DJ. 1997. A comparative analysis of allometry for sexual size dimorphism: Assessing Rensch's rule. American Naturalist 149(3):540-562.

Allen DS, Aspey WP. 1986. Determinants of social dominance in eastern gray squirrels (*Sciurus carolinensis*): A quantitative assessment. Animal Behaviour 34:81–89.

Altmann J. 1974. Observational study of behavior: Sampling methods. Behaviour 49:227–267.

Anderson M. 1986. Predation and primate evolution. Primates, 27(1):15-39.

Andersson M. 1994. Sexual selection. Princeton, New Jersey: Princeton University Press.

Bar Ziv E, Ilany A, Demartsev V, Barocas A, Geffen E, Koren L. 2016. Individual, social, and sexual niche traits affect copulation success in a polygynandrous mating system. Behavioral Ecology and Sociobiology 70(6):901-912.

Barelli C, Boesch C, Heistermann M, Reichard UH. 2008. Female white-handed gibbons (*Hylobates lar*) lead group movements and have priority of access to food resources. Behaviour 145:965–981.

Beaugrand JP, Payette D, Goulet C. 1996. Conflict outcome in male green swordtail fish dyads (*Xiphophorus Helleri*): Interaction of body size, prior dominance/subordination experience, and prior residency. Behaviour 133:303–319.

Berger J, Cunningham C. 1994. Predation, sensitivity, and sex: Why female black rhinoceroses outlive males. Behavioral Ecology 6(1):57-64.

Berger J, Gompper ME. 1999. Sex ratios in extant ungulates: Products of contemporary predation or past life histories? Journal of Mammalogy 80(4):1084-1113.

Bernstein IS. 1981. Dominance: The baby and the bathwater. Behavioral and Brain Sciences 4:419–429.

Bidau C, Martinez PA. 2016. Sexual size dimorphism and Rensch's rule in Canidae. Biological Journal of the Linnean Society 119:816-830.

Bondrup-Nielsen S, Ims RA. 1990. Reversed sexual size dimorphism in microtines: Are females larger than males or are males smaller than females? Evolutionary Ecology 4:261-272.

Boonstra R, Gilbert BS, Krebs CJ. 1993. Mating systems and sexual dimorphism in mass in microtines. Journal of Mammalogy 74(1):224-229.

Brockman DK. 1994. Reproduction and mating system of Verreaux's sifaka (*Propithecus vereauxi*) at Beza Mahafaly, Madagascar. PhD Dissertation, Yale University, New Haven.

Brockman DK. 1999. Reproductive Behavior of Female *Propithecus verreauxi* at Beza Mahafaly, Madagascar. International Journal of Primatology 20:375-398.

Cassini MH. 1999. The evolution of reproductive systems in pinnipeds. Behavioral Ecology 10(5):612-616.

Caudron AK. 1997. Pinnipeds social systems: A review. Mammalia 61:153-160.

Cavigelli SA, Dubovick T, Levash W, Jolly A, Pitts A. 2003. Female dominance status and fecal corticoids in a cooperative breeder with low reproductive skew: Ring-tailed lemurs (*Lemur catta*). Hormones and Behavior 43(1):166–179.

Chapais B. 1992. The role of alliances in social inheritance of rank among female primates. In: Harcourt AH, de Waal FBM, eds. Coalitions and Alliances in Humans and Other Mammals. Oxford: Oxford University Press.

Chase ID, Seitz K. 2011. Self-structuring properties of dominance hierarchies a new perspective. Advances in Genetics 75:51–81.

Chase ID, Tovey C, Spangler-Martin D, Manfredonia M. 2002. Individual differences versus social dynamics in the formation of animal dominance hierarchies. PNAS 99:5744–5749.

Cheverud JM, Dow MM, Leutenegger W. 1985. A quantitative assessment of phylogenetic constraints in comparative analyses: Sexual dimorphism in body weight among primates. Evolution 39(6):1335-1351.

Clutton-Brock TH. 2007. Sexual selection in males and females. Science 318:1882–1885.

Clutton-Brock TH, Harvey PH, Rudder B. 1977. Sexual dimorphism, socionomic sex ratio and body weight in primates. Nature, 269:797-800.

Clutton-Brock TH. 1989. Mammalian mating systems. Proceedings of the Royal Society of London B 236:339-372.

Coltman DW, Bowen WD, Wright JM. 1999. A multivariate analysis of phenotype and paternity in male harbor seals, *Phoca vitulina*, at Sable Island, Nova Scotia. Behavioral Ecology 10:169-177.

Cooper JD, Waser PM, Hellgren EC, Gabor TM, DeWoody JA. 2011. Is sexual monomorphism a predictor of polygynandry? Evidence from a social mammal, the collared peccary. Behavioral Ecology and Sociobiology 65(4):775-785.

Cox RM, Calsbeek R. 2009. Sexually antagonistic selection, sexual dimorphism, and the resolution of intralocus sexual conflict. The American Naturalist 173(2):176-187.

Cox RM, Skelly SL, John-Alder HB. 2003. A comparative test of adaptive hypotheses for sexual size dimorphism in lizards. Evolution 57:1653–1669.

Cullen TM, Fraser D, Rybczynski N, Schroder-Adams C. 2014. Early evolution of sexual dimorphism and polygyny in pinnipedia. Evolution 68(5):1469-1484.

Dale J, Dunn PO, Figuerola J, Lislevand T, Székely T, Whittingham LA. 2007. Sexual selection explains Rensch's rule of allometry for sexual size dimorphism. Proceedings of the Royal Society B 274:2971-2979.

Darwin C. 1871. The descent of man, and selection in relation to sex. London: J. Murray.

de Waal FB. 1986. The integration of dominance and social bonding in primates. Quarterly Review of Biology 61:459–479.

de Waal FB. 1989. Dominance 'style' and primate social organisation. In: Standen V, Foley R, eds. Comparative socioecology – The behavioral ecology of humans and other mammals. Blackwell Scientific Publications, Oxford. p. 243-364.

Devore I, Washburn SL. 1963. Baboon ecology and human evolution. In: Howell FC, Bourliere, editors. African ecology and human evolution. Chicago: Transaction Publishers. p 335-367.

Dewar RE, Richard AF. 2007. Evolution in the hypervariable environment of Madagascar. PNAS 104:13723–13727.

Dixson A, Anderson M. 2002. Sexual selection, seminal coagulation, and copulatory plug formation in primates. Folia Primatologica 73:63-69.

Dunham AE, HW Rudolf. 2009. Evolution of sexual size monomorphism: The influence of passive mate guarding. Journal of Evolutionary Biology 22:1376-1386.

Dunham AE, Maitner BS, Razafindratsima OH, Simmons MC, Roy CL. 2013. Body size and sexual size dimorphism in primates: Influence of climate and net primary productivity. Journal of Evolutionary Biology 26:2312-2320.

Dunham AE. 2008. Battle of the sexes: cost asymmetry explains female dominance in lemurs. Animal Behavior 76:1435-1439.

Eichmueller P, Thorén S, Radespiel U. 2013. The lack of female dominance in golden-brown mouse lemurs suggests alternative routes in lemur social evolution. American Journal of Physical Anthropology 150:158–164.

Ely J, Kurland JA. 1989. Spatial autocorrelation, phylogenetic constraints, and the causes of sexual dimorphism in primates. International Journal of Primatology 10:151-171.

Emery Thompson M. 2017. Energetics of feeding, social behavior, and life history in non-human primates. Hormones and Behavior 91:84–96.

Emlen ST, Oring LW. 1977. Sexual selection, and the evolution of mating systems. Science 197(4300):215-223.

Engle ET. 1926. The copulatory plug and the accessory genital glands of mammals. Journal of Mammology 7(2):119-126.

Estes RD. 1974. Social organization of the African Bovidae. In: Geist V, Walther F, editors. The behavior of ungulates and its relationship to management. Alberta, Canada: International Union for Conservation of Nature and Natural Resources. p 166-205.

Fairbairn DJ. 1997. Allometry for sexual size dimorphism: pattern and process in the coevolution of body size in males and females. Annual review of ecology and systematics 28:659-687.

Fairbairn DJ. 2007. Introduction: The enigma of sexual size dimorphism. In: Fairbairn DJ, Blanckenhorn WU, Székely T, editors. Sex, size and gender roles: Evolutionary studies of sexual size dimorphism. New York: Oxford University Press. p 1-10.

Ferguson SH, Higdon JW. 2006. How seals divide up the world: Environment, life-history, and conservation. Oecologia 150:318-329.

Ferrándiz-Rovira M, Lemaitre JF, Lardy S, López BC, Cohas A. 2014. Do pre- and post-copulatory sexually seleted traits covary in large herbivores? BMC Evolutionary Biology 14:79.

García-Navas V. 2017. Lack of evolution of sexual size dimorphism in Heteromyidae (Rodentia): The influence of resource defense and the trade-off between pre- and post-copulatory trait investment. Evolutionary Biology 44:56-68.

Garnier JN, Bruford MW, Goossens B. 2001. Mating system and reproductive skew in the black rhinoceros. Molecular Ecology 10(8):2031-2041.

Geist V and Bayer M. 1988. Sexual dimorphism in the Cervidae and its relation to habitat. Journal of Zoology, 214:45-53.

Gittleman JL, Van Valkenburgh B. 1997. Sexual dimorphism in the canines and skulls of carnivores: Effecs of size, phylogeny, and behavioural ecology. Journal of Zoology 242: 97-117.

Gordon AD. 2006. Scaling of size and dimorphism in primates II: Macroevolution. International Journal of Primatology 27(1):63-105.

Gowaty PA, Hubbell SP. 2005. Chance, time allocation, and the evolution of adaptively flexible sex role behavior. Integrative and Comparative Biology 45:931-944.

Hammerschlag N, Martin RA, Fallows C. 2006. Effects of environmental conditions on predator-prey interactions between white sharks (*Carcharodon carcharias*) and Cape fur seals (*Artocephalus pusillus pusillus*) at Seal Island, South Africa. Environmental Biology of Fishes 76:341-350.

Hand JL. 1986. Resolution of social conflicts: Dominance, egalitarianism, spheres of dominance, and game theory. Quarterly Review of Biology 61:201–220.

Heske EJ, Ostfeld RS. 1990. Sexual dimorphism in size, relative size of testes, and mating systems in North American voles. Journal of Mammology 71: 510-519.

Hewitt SE, Macdonald DW, Dugdale HL. 2009. Context-dependent linear dominance hierarchies in social groups of European badgers, *Meles meles*. Animal Behavior 77:161–169.

Hohenbrink S, Schaarschmidt F, Bünemann K, Gerberding S, Zimmermann E, Radespiel U. 2016. Female dominance in two basal primates, Microcebus murinus and Microcebus lehilahytsara: variation and determinants. Animal Behavior 122:145–156.

Holekamp KE, Smale L. 1991. Dominance acquisition during mammalian social development: The "inheritance" of maternal rank. Integrative and Comparative Biology 31:306–317.

Holekamp KE, Strauss ED. 2016. Aggression and dominance: an interdisciplinary overview. Current Opinion in Behavioral Sciences 12:44–51.

Isaac JL. 2005. Potential causes and life-history consequences of sexual size dimorphism in mammals. Mammal Review 35(1):101-115.

Jarman P. 1983. Mating system and sexual dimorphism in large terrestrial mammalian herbivores. Biological Reviews 58:485-520.

Jarman PJ. 1974. The social organization of antelope in relation to their ecology. Behaviour 48:215-267.

Jolly A. 1966. Lemur behavior. Chicago: University of Chicago Press.

Jolly A. 1984. The puzzle of female feeding priority. In: Small MF, editor. Female primates: Studies by women primatologists. New York: Liss. p 197-205.

Kappeler PM, Fichtel C. 2015. Eco-evo-devo of the lemur syndrome: did adaptive behavioral plasticity get canalized in a large primate radiation? Frontiers in Zoology 12:S15.

Kappeler PM, Ganzhorn JU. 1993. The evolution of primate communities and societies in Madagascar. Evolutionary Anthropology 2:159–171.

Kappeler PM, Shaffler L. 2008. The lemur syndrome unresolved: Extreme male reproductive skew in sifakas (*Propithecus verreauxi*), a sexually monomorphic primate with female dominance. Behavioral Ecology and Sociobiology 62(6):1007-1015.

Kappeler PM. 1990. Female dominance in *Lemur catta*: more than just female feeding priority? Folia Primatologica 55:92–95.

Kappeler PM. 1993a. Female dominance in primates and other mammals. Perspectives in Ethology 10:143–158.

Kappeler PM. 1993b. Variation in social structure: the effects of sex and kinship on social interactions in three lemur species. Ethology 93:125–145.

Kappeler PM. 1996. Causes and Consequences of Life-History Variation Among Strepsirhine Primates. The American Naturalist 148:868–891.

Kappler PM. 1990. The evolution of sexual size dimorphism in prosimian primates. American Journal of Primatology 21:201-214.

King WJ, Allainé D. 2002. Social, maternal, and environmental influences on reproductive success in female Alpine marmots (*Marmota marmota*). Canadian Journal of Zoology 80:2137-2143.

Kleiman DG. 1977. Monogamy in mammals. The Quarterly Review of Biology, 52(1): 39-69.

Koch F, Ganzhorn JU, Rothman JM, Chapman CA, Fichtel C. 2017. Sex and seasonal differences in diet and nutrient intake in Verreaux's sifakas (*Propithecus verreauxi*). American Journal of Primatology 79:1–10.

Kokko H, Jennions MD. 2008. Parental investment, sexual selection and sex ratios. Journal of Evolutionary Biology 21(4):919-948.

Koren L, Mokady O, Geffen E. 2006. Elevated testosterone levels and social ranks in female rock hyrax. Hormones and Behavior 49(4):470-477.

Kraus C, Heistermann M, Kappeler PM. 1999. Physiological suppression of sexual function of subordinate males: a subtle form of intrasexual competition among male sifakas (*Propithecus verreauxi*)? Physiology and Behavior 66:855–861.

Kruger O, Wolf JBW, Jonker RM, Hoffman JI, Trillmich F. 2014. Disentangling the contribution of sexual selection and ecology to the evolution of size dimorphism in pinnipeds. Evolution 68:1485-1496.

Kubzdela KS. 1997. Sociodemography in diurnal primates: The effects of group size and female dominance rank on intra-group spatial distribution, feeding competition, female reproductive success, and female dispersal patterns in white sifaka, *Propithecus verreauxi*. PhD Dissertation, University of Chicago.

Langbein J, Puppe B. 2004. Analysing dominance relationships by sociometric methods—a plea for a more standardised and precise approach in farm animals. Applied Animal Behavior Science 87:293–315.

Lawler RR, Richard AF, Riley MA. 2003. Genetic population structure of the white sifaka (*Propithecus verreauxi verreauxi*) at Beza Mahafaly Special Reserve, southwest Madagascar (1992--2001). Molecular Ecology 12:2307–2317.

Lawler RR, Richard AF, Riley MA. 2005. Intrasexual selection in Verreaux's sifaka (*Propithecus verreauxi verreauxi*). Journal of Human Evolution 48:259-277.

Le Boeuf BJ. 1986. Sexual strategies of seals and walruses. New Scientist, 1491:36-39.

Leigh SR, Shea BT. 1995. Ontogeny and the evolution of adult body size dimorphism in apes. American Journal of Primatology 36:37-60.

Leigh SR, Terranova CJ. 1997. Comparative perspectives on bimaturism, ontogeny, and dimorphism in lemurid primates. International Journal of Primatology 19(4):723-749.

Leighton DR. 1987. Gibbons: Territoriality and monogamy. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT, editors. Primate Societies. Chicago: The University of Chicago Press. p 146-154.

Leimberger KG, Lewis RJ. 2017. Patterns of male dispersal in Verreaux's sifaka (*Propithecus verreauxi*) at Kirindy Mitea National Park. American Journal of Primatology 79(7):e22455.

Lenth RV. 2016. Least-squares means: The R package lsmeans. Journal of Statistical Software 69(1)1-33.

Leutenegger WL, Cheverud J. 1982. Correlates of sexual dimorphism in primates: Ecological and size variables. International Journal of Primatology 3(4):387-402.

Leutenegger WL, Cheverud J. 1985. Sexual dimorphism in primates, the effect of size. In: Jungers WJ, editor. Size and scaling in primate biology. New York: Plenum Press. p 33-50.

Leutenegger WL, Kelly JT. 1977. Relationship of sexual dimorphism in canine size and body size to social, behavioral, and ecological correlates in anthropoid primates. Primates 18(1):117-136.

Lewis RJ, Bannar-Martin KH. 2012. The impact of cyclone Fanele on a tropical dry forest in Madagascar. Biotropica 44:135–140.

Lewis RJ, Kappeler PM. 2005. Seasonality, body condition, and timing of reproduction in *Propithecus verreauxi verreauxi* in the Kirindy Forest. American Journal of Primatology 67:347–364.

Lewis RJ, Rakotondranaivo F. 2011. The impact of Cyclone Fanele on sifaka body condition and reproduction in the tropical dry forest of western Madagascar. Journal of Tropical Ecology 27:429–432.

Lewis RJ, van Schaik CP. 2007. Bimorphism in male Verreaux's sifaka in the Kirindy Forest of Madagascar. International Journal of Primatology 28:159–182.

Lewis RJ. 2002. Beyond dominance: the importance of leverage. Quarterly Review of Biology 77:149–164.

Lewis RJ. 2009. Chest staining variation as a signal of testosterone levels in male Verreaux's Sifaka. Physiology and Behavior 96:586–592.

Lewis RJ. In press. Female power in primates and the phenomenon of female dominance. Annual Review of Anthropology.

Lindenfors P, Gittleman JL, Jones KE. 2007. Sexual size dimorphism in mammals. In: Fairbairn DJ, Blanckenhorn WU, Székely T, editors. Sex, size and gender roles: Evolutionary studies of sexual size dimorphism. New York: Oxford University Press. p 16-26.

Lindenfors P, Tullberg BS. 1998. 1998. Phylogenetic analyses of primate size evolution: The consequences of sexual selection. Biological Journal of the Linnean Society 64:413-447.

Lindenfors P. 2002. Sexually antagonistic selection on primate size. Journal of Evolutionary Biology 15(4):595-607.

Lovich JE, Gibbons JW. 1992. A review of techniques for quantifying sexual size dimorphism. Growth, Development and Aging 56:269-281.

Lüpold S, Tomkins JL, Simmons LW, Fitzpatrick JL. 2014. Female monopolization mediates the relationship between pre- and postcopulatory sexual traits. Nature Communications 5:1-8.

Mace GM. 1979. The evolutionary ecology of small mammals. Doctoral dissertation, University of Sussex.

Martin RD, Willner LA, Dettling A. 1994. The evolution of sexual size dimorphism in primates. In: Short RV, Balaban E, editors. The differences between the sexes. Cambridge: Cambridge University Press. p 159–200.

Martínez PA, Amado TF, Bidau CJ. 2014. A phylogenetic approach to the study of sexual size dimorphism in Felidae and an assessment of Rensch's rule. Ecosistemas 23(1): 27-36.

Martínez PA, Bidau CJ. 2016. A reassessment of Rensch's rule in tuco-tucos (Rodentia: Ctenomyidae: Ctenomys) using a phylogenetic approach. Mammalian Biology 81(1):66-72.

Mitani JC, Gros-Louis J, Richards AF. 1996. Sexual dimorphism, the operational sex ratio, and the intensity of male competition in polygynous primates. The American Naturalist 147(6): 966-980.

Norscia I, Palagi E. 2015. The socio-matrix reloaded: From hierarchy to dominance profile in wild lemurs. PeerJ 3:e729.

Packard JM, Babbitt KJ, Franchek KM, Pierce PM. 1991. Sexual competition in captive collared peccaries (*Tayassu tajacu*). Applied Animal Behaviour Science 29:319-326.

Palagi E, Antonacci D, Norscia I. 2008. Peacemaking on treetops: First evidence of reconciliation from a wild prosimian (*Propithecus verreauxi*). Animal Behavior 76:737–747.

Parga JA, Sauther ML, Cuozzo FP, Youssouf Jacky IA, Lawler RR, Sussman RW, Gould L, Pastorini J. Paternity in wild ring-tailed lemurs (*Lemur catta*): Implications for male mating strategies. American Journal of Primatology 78(12):1316-1325.

Parker GA, Lessells CM, Simmons LW. 2013. Sperm competition games: A general model for pre-copulatory male-male competition. Evolution 67:95-109.

Parker GI, Rubenstein DI. 1981. Role assessment, reserve strategy, and acquisition of information in asymmetric animal conflicts. Animal Behavior 29:221–240.

Pereira ME, Kaufman R, Kappeler PM, Overdorff DJ. 1990. Female dominance does not characterize all of the Lemuridae. Folia Primatologica 55:96–103.

Pereira ME. 1995. Development and social dominance among group-living primates. American Journal of Primatology 37:143–175.

Pereira ME. 2002. Agonistic interaction, dominance relation, and ontogenetic trajectories in ringtailed lemurs. Juvenile primates: Life history, development, and behavior Chicago: University of Chicago Press p:285–305.

Pérez-Barbería FJ, Gordon IJ, Pagel M. 2002. The origins of sexual dimorphism in body size in ungulates. Evolution 56(6):1276-1285.

Pérez-Barbería FJ, Gordon IJ. 2000. Differences in body mass and oral morphology between the sexes in the Artiodactyla: Evolutionary relationships with sexual segregation. Evolutionary Ecology Research 2:667-684.

Petty JMA, Drea CM. 2015. Female rule in lemurs is ancestral and hormonally mediated. Scientific Reports 5:9631.

Plant TM, Barker-Gibb ML. 2004. Neurobiological mechanisms of puberty in higher primates. Human Reproductive Update 10:67–77.

Plavcan JM, Van Schaik CP. 1997. Intrasexual competition and body weight dimorphism in anthropoid primates. American Journal of Physical Anthropology 103:37-68.

Plavcan JM. 2000. Inferring social behavior from sexual dimorphism in the fossil record. Journal of Human Evolution 39:327-344.

Plavcan JM. 2001. Sexual dimorphism in primate evolution. Yearbook of Physical Anthropology 44:25-53.

Plavcan JM. 2011. Understanding dimorphism as a function of changes in male and female traits. Evolutionary Anthropology 20:143-155.

R Core Team. 2016. A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.

Ralls K. 1976. Mammals in which females are larger than males. Quarterly Review of Biology 51:245–276.

Ralls K. 1977. Sexual dimorphism in mammals: Avian models and unanswered questions. The American Naturalist 111(981):917-938.

Rasambainarivo FT, Junge RE, Lewis RJ. 2014. Biomedical evaluation of Verreaux's sifaka (*Propithecus verreauxi*) from Kirindy Mitea National Park in Madagascar. Journal of Zoo Wildlife Medicine 45:247–255.

Rathbun GB. 1979. The social structure and ecology of elephant-shrews. Zeitschrift für Tierpsychologie 20:1–75.

Ravosa MJ, Meyers DM, Glander KE. 1993. Relative growth of the limbs and trunk in sifakas: heterochronic, ecological, and functional considerations. American Journal of Physical Anthropology 92:499–520.

Rensch B. 1960. The laws of evolution. In: The Evolution of Life. Chicago: University of Chicago Press. p 95-116.

Richard A, Heimbuch R. 1975. An Analysis of the Social Behavior of Three Groups of Verreauxi, Propithecus. In: Tattersali I, Sussman RW, editors. Lemur Biology. p. 313–333.

Richard A. 1974. Intra-specific variation in the social variation and ecology of Propithecus verreauxi. Folia Primatol 22:178–207.

Richard AF, Dewar RE, Schwartz M, Ratsirarson J. 2000. Mass change, environmental variability and female fertility in wild *Propithecus verreauxi*. Journal of Humn Evolution 39:381–391.

Richard AF, Dewar RE, Schwartz M, Ratsirarson J. 2002. Life in the slow lane? Demography and life histories of male and female sifaka (Propithecus verreauxi verreauxi). Journal of Zoology 256:421–436.

Richard AF, Nicoll ME. 1987. Female social dominance and basal metabolism in a malagasy primate, *Propithecus verreauxi*. American Journal of Primatology 12:309–314.

Richard AF. 1978. Behavioral Variation: Case Study of a Malagasy Lemur. Bucknell University Press.

Richard AF. 1992. Aggressive competition between males, female-controlled polygyny and sexual monomorphism in a Malagasy primate, *Propithecus verrauxi*. Journal of Human Evolution 22:395-406.

Rodman PS, Mitani JC. 1987. Orangutans: Sexual dimorphism in a solitary species. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT, editors. Primate Societies. Chicago: The University of Chicago Press. p 146-154.

Rowell TE. 1974. The concept of social dominance. Behavioral Biology 11:131–154.

Schmidt-Nielsen K. 1984. Scaling: Why is animal size so important? Cambridge: Cambridge University Press.

Schulte-Hostedde AI, Millar JS. 2002. 'Little chipmunk' syndrome? Male body size and dominance in captive yellow-pine chipmunks (*Tamias amoenus*). Ethology 108:127–137.

Shanahan T. 2011. Phylogenetic inertia and Darwin's higher law. Studies in History and Philosophy of Biological and Biomedical Sciences 42(1):60-68.

Shine, R. 1988. The evolution of large body size in females: a critique of Darwin's "fecundity advantage" model. American Naturalist 131:124–131.

Sibly RM, Zuo W, Kodric-Brown A, Brown JH. 2012. Rensch's rule in large herbivorous mammals derived from metabolic scaling. The American Naturalist 179(2):169-177.

Sicotte P. 2002. The function of male aggressive displays towards females in mountain gorillas. Primates 43:277–289.

Smith RJ, Cheverud JM. 2002. Scaling of sexual dimorphism in body mass: a phylogenetic analysis of Rensch's rule in primates. International Journal of Primatology 23(5):1095-1135.

Stevens RD, Platt RN. 2015. Patterns of secondary sexual size dimorphism in New World Myotis and a test of Rensch's rule. Journal of Mammalogy 96(6):1128-1134.

Strier KB, Chaves PB, Mendes SL, Fagundes V, Di Fiore A. 2011. Low paternity skew and the influence of maternal kin in an egalitarian, patrilocal primate. PNAS 108(47):18915-18919.

Strier KB. 1990. New World primates, new frontiers: insights from the woolly spider monkey, or muriqui (*Brachyteles arachnoides*). International Journal of Primatology 11(1):7-19.

Surbeck M, Hohmann G. 2013. Intersexual dominance relationships and the influence of leverage on the outcome of conflicts in wild bonobos (*Pan paniscus*). Behavioral Ecology and Sociobiology 67:1767–1780.

Székely T, Freckleton RP, Reynolds JD. 2004. Sexual selection explains Rensch's rule of size dimorphism in shorebirds. PNAS 101(33):12224-12227.

Tennenhouse Em. 2015. The influence of growth patterns on sexual size monomorphism in lemurs. Journal of Evolutionary Biology 28:1670-1681.

Tilden CD, Oftedal OT. 1995. The bioenergetics of reproduction in prosimian primates: Is it related to female dominance? In: Alterman L, Doyle GA, Izard MK, eds. Creatures of the Dark. Springer, Boston, MA. p 119–131.

Tilden CD, Oftedal OT. 1997. Milk composition reflects pattern of material care in prosimian primates. American Journal of Primatology 41:195–211.

Trivers RT. 1972. Parental investment and sexual selection. In: Campbell B, editor. Sexual Selection and the Descent of Man, 1871-1971. New York: Aldine Publishing Company. p 136-179.

van Noordwijk MA, van Schaik CP. 2009. Intersexual food transfer among orangutans: do females test males for coercive tendency? Behavior Ecology and Sociobiology 63:883–890.

van Schaik CP, Kappeler PM. 1996. The social systems of gregarious lemurs: lack of convergence with anthropoids due to evolutionary disequilibrium? Ethology 102:915–941.

Vanpe C, Kjellander P, Galan M, Cosson JF, Aulagnier S, Liberg O, Hewison AJM. 2007. Mating system sexual dimorphism, and the opportunity for sexual selection in a territorial ungulate. Behavioral Ecology 19(2):309-316.

vom Saal FS. 1989. Sexual differentiation in litter-bearing mammals: Influence of sex of adjacent fetuses in utero. Journal of Animal Science 67:1824-1840.

Voss R. 1979. Male accessory glands and the evolution of copulatory plugs in rodents. Occasional Papers of the Museum of Zoology University of Michigan 689:1-17.

Weckerly FW. 1998. Sexual-size dimorphism: Influence of mass and mating systems in the most dimorphic mammals. Journal of Mammology 79(1):33-52.

Wimmer B, Kappeler PM. 2002. The effects of sexual selection and life history on the genetic structure of redfronted lemur, *Eulemur fulvus rufus*, groups. Animal Behavior 64:557-568.

Wolff JO. 2007. Social biology of rodents. Integrative Zoology, 2:193-204.

Wright PC. 1999. Lemur traits and Madagascar ecology: coping with an island environment. American Journal of Physical Anthropology 110(29):31-72.

Yoccoz NG, Mesnager S. 1998. Are alpine bank voles larger and more sexually dimorphic because adults survive better? Oikos 82(1):85-98.